AGONISTIC BEHAVIOR, SOCIAL DOMINANCE, AND PREDATOR EVASION OF *ONCORHYNCHUS MYKISS* FROM LAKE AND STREAM PARENTS AN EVALUATION OF LACUSTRINE REFUGES AS A CONSERVATION STRATEGY FOR THREATENED OR ENDANGERED SALMONIDS

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A

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Abstract

The possibility of lakes providing temporary natural refugia for endangered salmonid populations, creating an alternative to hatchery propagation, is the context for this research. To investigate this possibility resident trout (*Oncorhynchus mykiss*) derived from a population that had been sequestered in a lake for seventy years were compared to fish from their founding anadromous steelhead trout population as well as to hybrid crosses of the two populations. Comparisons were made in the areas of aggression, dominance and predator evasion. In aggression trials the lake-derived population chased more than stream-derived *O. mykiss* at two life stages, age-0 and age-1. Lake-derived fry and the lake x stream hybrid fry also chased more than the stream x lake hybrid fry. Fin conditions (dorsal and pectoral fin lengths, an index of aggression) did not differ significantly. In dominance acquisition the stream x lake hybrid were least frequently dominant of all the crosstypes, and stream-derived parr were less dominant than lake-derived parr. Avoidance of a Dolly Varden predator by fry showed that the stream x lake hybrids achieved the highest survival rates. Seventy years of sequestration in a lake may be adequate time for divergence in aggressive behavior, social dominance and predator evasion between lake-resident and stream, *O. mykiss* populations.

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Introduction

In the past decade, there has been much concern over the loss of suitable stream habitat from industrialization and agricultural practices in the Pacific Northwest, resulting in declining Pacific salmon populations returning to spawn in their native streams (Lichatowich 1999). The rate and quantity of habitat destruction and fish mortality demonstrated a need for human intervention to slow the effects of habitat destruction on salmonid populations. Restoration and mitigation efforts have largely involved increasing the number of salmon produced through artificial propagation (i.e. hatcheries).

Historically, fish hatcheries were seen as a solution to the problem of declining salmon returns that did not necessitate stopping or reversing industrial development (Lichatowich 1999). However, due to poor artificial culture practices such as selective breeding, use of non-local stock, and inadequate disease control, early fish hatcheries produced fish that had low survival and interfered with wild populations (Allendorf & Phelps 1980; Evenden et al. 1993; Mitchum & Sherman 1981; Olla et al. 1994; Reisenbichler & Rubin 1999).

Great improvements in aquaculture practices have enabled the production of large numbers of salmon, and artificial culture has been embraced by most federal and state agencies and private non-profit organizations for conservation purposes as well as to provide fishing opportunities. Survival of emergent fry and yearlings in captivity far surpasses natural survival by eliminating principle causes of mortality such as starvation and predation. Hatcheries are already in place, and produce substantial numbers of smolts. However, there are still questions about the survival of hatchery populations as well as their contribution to natural productivity (Chilcote 2003; Chilcote et al. 1986; McLean et al. 2003; Nickelson et al. 1986; Nickelson 2003).

Different types of hatcheries have different goals and therefore different criteria for success. Production hatcheries focus on creating fish for harvest and are therefore judged on the amount of fish they contribute to the fishery over the cost of production (Seelbach 1987), while conservation hatcheries are judged on their ability to aid in conservation of natural stocks (Flagg et al. 2000). Production hatcheries focus on

providing fish for harvest cheaply, so size selection, unequal family sizes and non-natural hatchery settings may be experienced, these culture practices may alter the gene frequencies of the hatchery population making it different from the wild populations.

Conservation hatcheries work to minimize the genetic and learned differences between hatchery and wild populations. This is important because the ultimate goal for conservation hatcheries is the future ability of the population to maintain itself without intervention. By keeping the hatchery population as closely related to the wild population as possible it is possible to minimize the effect of a hatchery on a wild population. However, if hatchery-reared fish exhibit reduced fitness (Chilcote et al. 1986) or inappropriate spawning behaviors (Berejikian & Tezak 2001; Berejikian et al. 2001a) then interventions may be continually required.

Some of the methods used by conservation hatcheries include the use of locally adapted wild populations to found hatchery populations, as well as avoiding selective breeding (e.g. for body size and run timing). In some cases wild-origin returns also contribute each generation to the hatchery stock. Physical alterations to the hatchery can also make the hatchery environment closer to that which fish encounter in a natural stream (Berejikian et al. 1996; Berejikian et al. 2000; Berejikian et al. 2001b; Berejikian et al. 1999; Flagg et al. 2000).

Physical changes to the hatchery include mid-water feeding, reduced fish densities and handling, along with addition of natural cover and substrate. With this more "natural" environment it is thought that salmon in culture can maintain the same habits (i.e. use of cover, blending into substrate) as wild fish in avoiding aggressive competition, demonstrating dominance or submission, and defending territories. Experiments comparing dominance acquisition in steelhead raised in hatchery environments enriched with woody in-water structure, camouflage cover, and mid-water food delivery, to steelhead raised in conventional hatcheries indicated that steelhead raised in the enriched environment socially dominated those grown in conventional hatcheries (Berejikian et al. 2000; Berejikian et al. 2001b). Hatchery coho (*Oncorhynchus kisutch*) grown in a conventional hatchery were more aggressive than either hatchery

coho grown in natural stream environments or wild coho (Rhodes & Quinn 1998). A more direct behavioral addition to conservation hatcheries has been to condition fish in culture to avoid predators. These efforts have been successful in laboratories (Berejikian et al. 2003; Berejikian 1995; Healey & Reinhardt 1995), but improved survival in the wild due to this conditioning has not been verified.

In recent years captive rearing of salmonids has emerged as a measure to preserve populations at risk of extinction (Flagg et al. 1992; Waples & Do 1994). This intervention focuses on augmentation of a population rather than on production of smolts for ultimate harvest. Fish are raised from egg to adult in captivity and released to reproduce in the wild. These techniques may be prohibitively expensive and may cause undesirable genetic change even though natural mate selection has occurred.

The purpose of this study is to determine if lakes and reservoirs as refuges could provide an alternative to hatcheries or captive rearing for the conservation of threatened or endangered salmonid stocks. Temporarily sequestering populations in natural lacustrine habitats may be one approach to maintaining fitness characteristics populations while the degraded freshwater environments that led to reduced productivity have been sufficiently restored (reviewed by Thrower et al. 2003). Salmonids in an isolated lacustrine refuge would not be subjected domestication selection pressures associated with artificial culture that can occur within several generations (Reisenbichler and Rubin 1999). Fish produced from such a "natural" environment might be better candidates for reintroduction to a restored habitat because they would not acquire the unnatural behavior patterns learned or selected for in hatchery culture. Fish produced from such a "natural" environment might be better candidates for reintroduction to a restored habitat because they would not acquire the unnatural behavior patterns learned or selected for in hatchery culture.

A successful refuge for imperiled populations must provide habitat sufficient to lead to increased population abundance as well as reduce the mortality experienced by an anadromous population in the migratory corridor (e.g. Columbia River power system)

and in the ocean. In addition, refugia offering environmental characteristics (temperature, predator assemblages, competitors) similar to the ancestral stream habitats may further benefit the maintenance of adaptive characteristics (Taylor & Larkin 1986). Local adaptation to lake and stream environments of reciprocally transplanted threespine sticklebacks *(Gasterosteus aculeatus)* demonstrated that growth was best for each in their ancestral environment (Hendry et al. 2002) indicating that adaptive divergence to the stream or lake environment had occurred.

In order to achieve high fitness, anadromous salmonids must successfully smolt and migrate, be successful in aggressive contests for nesting territories and mates, obtain food and territories, as well as avoid predators. Natural selection may shape each of these traits to varying degrees, and environmental differences between lacustrine refugia and natural stream habitats may determine the extent to which sequestered populations diverge from their founder population. If generations of sequestration in a lake severely reduces the fitness of a population after reintroduction to its natal stream and ocean habitats then the use of lakes would do little to preserve imperiled populations. General adaptations to a lake environment that might be a concern include the loss of anadromy or smoltification (Northcote 1981), an inability to drift feed and decreased competitive ability, as well as changes in predator avoidance.

Sequestration for generations in a lake may not be sufficient to repress migratory ability of anadromous salmonids. A well-known example of this is the Redfish Lake sockeye salmon (*Oncorhynchus nerka*) population, which lived and reproduced in the lake after a dam blocked all migration from the lake to the ocean (Northcote 1997; Ricker 1938). Approximately twenty years after its construction, the dam was removed and a few years later the anadromous population returned. Residual sockeye were probably the source of the returning anadromous population and the reason that the population did not become extinct (Hauck 1955). The Redfish Lake sockeye salmon example suggests that lakes offer a possibility for a productive refuge. Preliminary work on the migratory behavior of the *O. mykiss* population studied here shows that average (over two cohorts) marine survival of smolts artificially produced from anadromous and from lake-resident

segments of a population was 2.66% and 0.105% respectively (Thrower et al. 2004). Smoltification rates were 68% (stream population) and 50% (lake population) for fish raised in artificial culture.

During the freshwater juvenile stages of salmonids food requirements and predation risks are great. Gaining access to food and cover from predation are important skills for juvenile survival. Salmon will learn predator evasion (Berejikian 1995) and how to feed in new environments (Berejikian 1995; Paszkowski & Olla 1985), but intense competition for resources may be the most important challenge. Successful foraging in a stream requires defense of an optimal territory (Fausch 1984). However, for foragers in open water (lakes, ocean, estuaries) time spent in territory defense could result in high energetic costs with little caloric return (Biro et al. 1997).

Fish sequestered in a lake may not have the competitive ability of their stream counterparts (Taylor 1990). In streams, competition for optimal territories can be fierce (Keeley 1998), whereas in still water, a lack of territoriality has been observed in brook charr (*Salvelinus fontinalis*) (Biro et al. 1997). Factors that affect territory size include prey abundance (Keeley & Grant 1994; Slaney & Northcote 1974) and body size (Keeley & Grant 1994; Keeley & McPhail 1998). Thus, the amount of territory needed and what defines a good territory could be different in different environments. However, Keeley and McPhail (1998) found that current velocity had no significant effect on territory size in juvenile steelhead trout. The behaviors by which a good territory is defended or won by an individual may also differ between populations. The high energetic cost of station-holding in a fast moving current (Fausch 1984) could translate into different methods of communication and station-holding. Swain & Holtby (1989) discovered that stream coho were more aggressive than lake coho and concluded that the difference between the lake population and the population inhabiting the lake's tributary were due to genetic divergence of the populations.

It is unknown whether an anadromous stream population transplanted into a lake for conservation purposes would acquire a less competitive behavior and whether this behavior would persist. Inability to defend a territory could cause a divergence in the

populations as selection in a stream favors fish that can defend a territory while fish that cannot are relegated to sub-optimal areas for drift feeding and face increased exposure to predation in the stream. In the lake environment a reduced tendency to defend a territory might not be associated with lower growth and survival and might reduce an individual's energetic costs, therefore fish exhibiting less aggression might contribute relatively more to the next generation. This research evaluated the risks of conservation programs using lacustrine refuges by comparing behavior of fish derived from two lines—one derived from a stream population of *O. mykiss* and one derived from a population transplanted from the stream to an isolated lake 70 years earlier, to determine if genetic divergence occurred between the two populations. As a conservation tool the use of refuges would be for a limited period of time before re-introduction into the streams would be performed. Therefore the behaviors of hybrids created from these two strains are also important and were investigated.

Description of Study Site and Populations

Steelhead derived from the Sashin Creek population represents the 'stream' population in this study. Sashin Creek is located in southeast Alaska on Baranof Island (56° 23'N 134° 44'W). The creek is approximately 4 km long (Kline et al. 1989) and supports a small steelhead and rainbow trout population. Smolting and migration occurs from April to May (Kline et al. 1989), smolts are approximately 3-4 four years old and spend 2 –3 years in the sea before returning (Thrower et al. 2003). The population may experience predation in Sashin Creek from Dolly Varden, coast range sculpin (*Cottus aleuticus*), coho, and pink salmon (*O. gorbuscha*) as well as rainbow trout (Kline et al. 1989). Sashin Creek arises in a 1340 ha watershed including two lakes, Sashin and Round (Hard & Heard 1999; Kline et al. 1989). Stream flows in Sashin Creek are variable, with flooding events occurring after snowmelts and heavy sustained rains. Two waterfalls block upstream migration and One thousand, two hundred meters of Sashin Creek is available for habitation by anadromous steelhead below the first impassable waterfall (30 m high) (Kline et al. 1989)(Figure1).

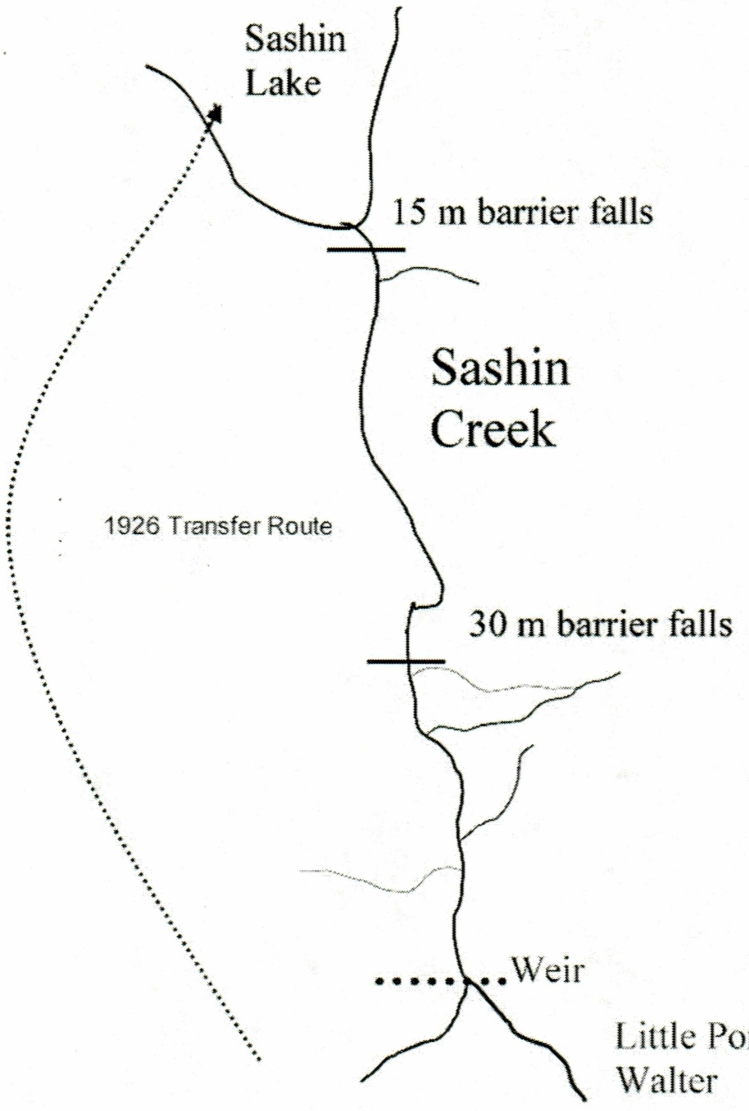

Figure 1: Location of Sashin Lake, Sashin Creek and waterfalls. Sashin Lake flowing into Sashin Creek which enters seawater at Little Port Walter. Drawn on the map are the locations of the two barrier waterfalls. Also depicted is the route taken in 1926 transplant of the stream *O. mykiss* to the lake.

A mixture of Sashin Creek O. mykiss, probably consisting of both the anadromous (steelhead) and resident (rainbow trout) forms, were transplanted into Sashin Lake approximately seventy years ago (Anonymous 1938). The transplant was successful and a substantial *O. mykiss* population became established in the lake. There is evidence that the lake population still produces *O. mykiss* that emigrate as smolts from the lake and migrate to the ocean. Genetic analysis comparing the Sashin Lake population to its founding stream population showed a loss of some rare alleles in the lake population, however the thriving lake population did not show evidence of excessive inbreeding (Thrower et al. 2003). No fish predators other than older *O. mykiss* exist in Sashin Lake.

Having a sequestered population present in Sashin Lake that has been reproductively isolated for seventy years provides an opportunity to study the effects of transplanting stream populations into lakes. The Sashin *O. mykiss* populations described in this study often defy rigid definitions of steelhead and rainbow trout. To avoid confusion the fish will be referred as *O. mykiss* and will be defined by their ancestral origins (lake or stream).

In 1996, an experimental population was created when NOAA Fisheries scientists sampled *O. mykiss* adults from Sashin Lake and Sashin Creek. This parent population was artificially spawned using gametes from 32 male and 30 female lake-fish, and 5 male and 18 female stream-fish to create F_1 offspring lines. The offspring from these crosses were raised in captivity at the Little Port Walter research station. In 2001 and 2002, scientists created a F_2 generation from *O. mykiss* that had undergone smoltification and grown to maturity. Four main cross types were produced from these spawnings and are the subjects for the following experiments:

Lake population (female) X Lake population (male): pure cross
Lake population (female) X Stream population (male): hybrid
Stream population (female) X Stream population (male): pure cross
Stream population (female) X Lake population (male): hybrid

Reciprocal hybrid crosses of the two populations will be referred to according to their parental cross female x male (e.g. 'stream x lake' refers to a fish with a stream mother

and a lake father). The reciprocal crosses were made in culture in 2001 and 2002 by breeding F_1 Sashin Lake *O. mykiss* with F_1Sashin Creek *O. mykiss.*

Ten different families represented each crosstype, the families were created from the F_1 generation *O. mykiss* that had gone through smoltification and sexual maturation in culture. The ten families per crosstype were raised in individual vertical raceways, in the vertical raceways the fish experienced identical feeding regimens and in most cases the same density of 550 fry, although through disease and escape some of the raceways had lower populations by the time of the experiment. Due to the low densities in the fry population only four families (which all contained 550 fry) from each crosstype were used to represent each crosstype for trials using fry. For the parr trials all ten families were used to represent each crosstype. Egg size measurements performed on the females producing the broodstock used in this experiment indicated no difference in egg size between any of the crosstypes tested, suggesting that early development size inequalities were not source of aggressive advantages (personal observation). Thus, the different crosstypes all experienced the same rearing environment and therefore differences seen between the crosstypes can be attributed to genetic instead of environmental effects.

The focus of this experiment is to determine if divergence has occurred between the stream and lake populations. Direct observations of behavior and physical measurements have been used to compare hatchery and wild fish and similar experiments would be beneficial for determining if genetic differences exist between lake and stream-derived *O. mykiss.* The experimental design and behaviors observed in published hatchery vs. wild experiments, which focus on aggression, social dominance and predator avoidance, will be used as templates for identifying hypothesized differences in behavior between lake- and stream-derived fish (Berejikian 1995; Berejikian et al. 1996; Berejikian et al. 2000; Berejikian et al. 1999; Fenderson et al. 1968; Keenleyside & Yamamoto 1962; Kindschi et al. 1987, Mesa 1991; Rosenau & McPhail 1987, Soderberg & Meade 1987). These studies provide good indications of which behaviors are important to the survival of a population, can be dependably observed and have a heritable (Swain & Riddell 1990) as well as an environmental component (Fenderson et al. 1968). In many

studies the hatchery population being compared to the wild population is not locally founded, and thus do not separate the environmental component from the genetic differences associated with local adaptation of the population. However, these studies do mimic real introductions that may occur and their possible effects on wild populations. Confounded results were avoided in this experiment because the lake population was founded exclusively by the stream population.

Aggressive Behavior

The environment of hatchery culture affects aggressive behavior. Swain and Riddell (1990) found hatchery coho salmon to be more aggressive than wild coho from a geographically proximate stream. Berejikian et al. (1996) saw more aggressive behavior in wild steelhead trout fry when compared to a hatchery population that was derived from the same wild population generations before. The effect of rearing environment was also tested by Berejikian et al (1996) who found that hatchery steelhead raised in natural stream channels performed more aggressive acts than either wild steelhead raised in a natural stream channel or hatchery steelhead raised in a conventional hatchery. In experiments performed by Mesa (1991), hatchery cutthroat trout were more aggressive than the corresponding wild population although the early rearing environment differed between the two populations and may have accounted for the differences detected.

Aggressive behavior is both a learned and inherent adaptive trait (Rhodes & Quinn 1998, 1999; Swain & Riddell 1990). Direct observations of aggressive behavior allow for comparisons of levels of aggression, time spent in aggressive activities, as well as comparisons of what types of aggressive behavior populations exhibit. There are many reasons why the aggressiveness of individuals in a population is important. Aggressive behavior gains fish access to food and later in life mates, making it an important component of the fitness of a fish. However, energy allocated to aggressive acts is energy that is not used for growth or reproduction (Fausch 1984). Also, aggression can make fish more vulnerable to predation (Dill & Fraser 1984).

Differences in aggression between hatchery and wild populations could negatively affect the wild populations upon reintroduction. Aggressive hatchery salmon may engage wild salmon in tiring contests, force them out of territories, reproduce with wild fish and change the aggressiveness of the population's offspring to a level that is not suitable for the wild environment. For either conservation and or supplementation programs this could diminish the effectiveness of hatcheries because interactions between the wild and hatchery fish could decrease the number of wild fish surviving during freshwater stages or could lead to hatchery fish replacing instead of enhancing wild populations (McMichael et al. 1999; Nickelson et al. 1986).

Fin Condition

In addition to direct observations of aggressive behavior indexes such as fin condition can be used to quantify accumulative effects of aggression on the morphology of populations. Previous work has been performed on detecting differences between the fin condition of hatchery and wild salmonids. The degraded dorsal fins of fish reared in hatchery systems were seen to be a result of crowded conditions as well as elevated levels of nipping (Soderberg & Meade 1987, Wagner 1996). Kindschi et al. (1987) developed a statistical index that allows for quantification of fin loss due to nipping. This index has been used to determine differences in aggression among populations (Siikavuopio et al 1996, Wagner 1996).

Unlike direct observations of aggression, fin condition can yield information on the aggression of a population over a long period of time. Fin nipping occurs in agonistic exchanges when actual contact is made. It occurs in the wild but has received greater attention since the emergence of hatcheries because hatchery fish have exhibited fins that are ragged due to aggressive action in captivity (Soderberg and Meade 1987). However, fin condition only reflects the amount of nipping that occurs and not other aggressive behaviors such as chasing or threat displays.

Social Dominance

Social dominance is a behavior that has been observed in the freshwater stage of most salmonid populations. Once dominance is established, certain advantages are earned by the dominant fish, such as less frequent attacks or nips by other fish, position in an optimal feeding station, increased growth (Fausch 1984), and access to mates (Berejikian & Tezak 2001). Dominance in size-matched fish is established through physical encounters which include displays of size and aggressive attacks. Observations of these encounters have been well documented (Rosenau & McPhail 1987; Taylor & Larkin 1986). There are also recorded subordinate displays that fish will perform to avoid aggressive attacks by a dominant fish. These are characterized by a closed mouth and decreased flare of fins (Swain & Riddell 1990).The dominant fish can usually be identified by its optimal feeding position, the number of attacks it delivers, and the relatively few attacks that it receives (Vosyliene et al. 1993). Dominance establishment in salmonids can also be seen later in life during spawning when large, aggressive males will gain the ability to spawn with females (Berejikian & Tezak 2001). Social dominance can be observed and recorded by observing an individual fish's ability to have supremacy over others by gaining access to food, mates, or optimal habitat.

In a study that did not control for the early life habitat of wild and hatchery fry (Fenderson et al. 1968) reported that hatchery reared Atlantic salmon (*Salmo salar*) established dominance more frequently, and dominant hatchery salmon performed more aggressive acts than the wild populations they were derived from. However, in an experiment performed by Berejikian et al (1996) that controlled for early life habitat, wild *O. mykiss* fry were more aggressive and acquired dominance more often than the hatchery fish, but when the hatchery fry were given a size advantage (3.0-4.5%) the hatchery fish won more challenges. McMichael et al (1999) observed that in a natural stream system, hatchery *O. mykiss* were seen to displace wild steelhead in their natural streams. Hatchery *O. mykiss* were also seen to win the majority of contests; in this experiment the hatchery steelhead were often larger than the wild steelhead (McMichael et al. 1999).

The effect of size on dominance acquisition has been well studied (Abbott et al. 1985; Keeley & McPhail 1998). In general, larger salmonids acquire dominance more frequently; however, this larger size may be consequence of behavior ("fierceness") that promotes social dominance rather than the cause of social dominance (Huntingford et al. 1990). This effect of size is an important finding because at release hatchery fish are usually larger than their cohorts in the wild and if social dominance is a product of size, wild fish could be at a disadvantage in competing with released hatchery fish (Rhodes & Quinn 1998).

Predator Avoidance

Predator avoidance is important because survival in the wild is directly dependent on it. Upon release, fish grown in captivity are naïve to predation and can exhibit behaviors that put them at high risk of capture. Predator avoidance can improve with experience. Genetic differences have been observed between wild and locally derived hatchery populations of *O. mykiss* in predator avoidance (Berejikian 1995); naïve wild *O. mykiss* fry avoided a predator more often than did naïve hatchery fry. Experience was also tested, and the results showed wild-experienced fry to be the best at avoiding predation followed by wild-naïve fry, hatchery-experienced fry, and finally hatchery-naïve fry. In laboratory experiments, experience does increase the survival of hatchery fry but not to the degree that being wild does.

Even if genetic differences do not exist between hatchery and wild populations, there is little opportunity for learned anti-predatory behaviors to develop in regular hatchery systems. The size of hatchery fish at release can also play an important role as the general larger body of hatchery fish means that they are no longer prey size for some predators, and size itself is a powerful component to the establishment of social dominance (Abbott et al. 1985). Another concern is the behaviors of hybrid fish. A study by (Johnsson & Abrahams 1991), found wild x hatchery hybrid steelhead (developed from a native wild and foreign hatchery brood) did not exhibit normal anti-predatory behavior by continuing to forage while predators were present.

The ability to avoid a predator is of obvious importance to an emerging fry. A large portion of mortality for emergent fry may be predator induced. Antipredatory behavior varies among species (Healey & Reinhardt 1995). In nature, trade-offs exist between foraging for food and avoiding predation. Foraging tactics of *O. mykiss* change in response to predation pressure (Tabor & Wurtsbaugh 1991). Behavioral differences in salmonid populations can be driven by the lack or presence of certain predator types. Thus exposure to predation is a useful tool in identifying possible differences in populations (Berejikian 1995).

Methods and Results:

Apparatus

Paired elevated experimental flumes were used in all behavior trials. Each flume (740 cm long x 123 cm wide x 55 cm high) held 10 equally spaced 208 L aquariums. The aquarium dimensions were 120 cm long x 32 wide x 53 cm high. Glass windows (48 cm x 47 cm) allowed for viewing of all areas inside the flume. The flume was filled with filtered water from Sashin Creek, and standpipes controlled the water level in the flume. The water flowing in the flume maintained constant temperature among all aquariums during the observations. The temperature of the water, recorded twice daily, was determined by the temperature of Sashin Creek.

The individual aquaria had their own water flow that passed through two filters and a head tank. The flow for the aquaria was controlled with two valves, one on each of two inflow tubes. The water flowed into each aquarium through a mid-water anterior-stationed flow tube and out through a mid-water siphon at the posterior end of the aquaria, creating an 'upstream' and 'downstream' effect within the aquarium. Flow was measured every other day (average1.4 L/sec, σ .06).

Black curtains, hung from the ceiling light source to the lower edge of the flume, created a blind. During acclimation, the curtains were clipped to the edge of the flume allowing no light to enter. During observation, the curtains were rolled up to water level. The lighting came from inside the flume so that observers were not visible to the fish if

they were least 50 cm away from the flume. The outside room was kept dark during the entire acclimation and observation period. The photoperiod was set to mimic the natural photoperiod (sixteen hours of daylight and eight hours of darkness).

For all behavior experiments the fish were allowed to acclimate before the trials began. The acclimation periods were approximately 18 hours for aggression trials and 38 hours for dominance trials. During the acclimation period the fish were fed twice: the first feeding occurred on the acclimation day and the second three hours prior to observation.

The fish were also fed immediately prior to observations. A food-water slurry consisting of the supernatant of 100g Moore Clark mash suspended in 5,000 ml water was introduced at each feeding to alert the fish in the aquarium to the presence of food. The parr were fed 0.5 grams of #2 crum Moore Clark ™, the fry 0.01 grams of Moore Clark™ mash at each feeding.

Aggressive Behavior Trials:

The total number of chases, nips, charges, approaches, and displays by fry or by parr in each aquarium were recorded and the durations of chases, charges, approaches, and displays were recorded (Table 1).

Table 1. Experimental design for the study of aggression by fry or by parr. Shows the number and crosstype of fry or parr observed in each replicate trial in an aquarium as well as the number of replicate trials of observations of fry or parr in aquaria.

	Within Lake-derived population	Within Stream-derived population	Stream (mother) by Lake (father) hybrids	Lake (mother) by Stream (father) hybrids	Combined Lake- and Stream-Derived
Fry trials	4 fry, 39 replicates	4 fry, 40 replicates	4 fry, 40 replicates	4 fry, 41 replicates	
Parr trials	2 parr, 35 replicates	2 parr, 37 replicates			1 Lake- and 1 Stream-Derived parr, 38 replicates

Each aquarium, not each fish, was counted as a replicate. The population assigned to each aquarium was randomized to reduce the potential for bias associated with random aquarium effects and observer/crosstype interaction effects. Fish in each aquarium were netted from their family-specific raceways and size-matched within 3 mm (parr), and 1.5 mm (fry) before being randomly assigned to an aquarium. Members of the same family were not assigned to the same aquaria to avoid any effects of kinship on behavior. This was possible because all families were raised in family-specific raceways and only removed from these raceways at the time of observation.

The J-watcher program™ was used to record the number of nips and the number and duration of charges, lateral displays, and chases in each aquarium (Table 2).

Table 2. Definitions of aggressive behavior

Behavior	Description of action
Approach	Movement of one fish toward another. Often this movement resulted in the fish moving into the territory of another fish
Charge	Fast swimming directly toward another fish, sometimes resulting in ramming
Chase	Longer than an approach and results in the displacement of chased fish from its original position
Nip	Any open mouth contact or near contact with biting motion
Display	Body of fish rigid with fins extended, possibly gaping

After initial observations, the aquaria were left for two hours before a second set of observations of the same duration were performed. The total actions of the two observations were added together for each replicate aquarium. After the trials were completed the fish were removed from the aquaria, the aquaria were cleaned, and new fish were introduced for subsequent trials.

Parr were observed in pairs, either two lake-derived parr (N=35 trials) two stream-derived parr (N=37), or one stream- and one lake-derived parr (N=38; Figure 2). Each observation was ten minutes in duration. One of the fish in each aquarium was marked with an adipose fin clip (ad-clip) so that individual fish dominance behavior could be recorded. The aquarium and ad-clip assignments were randomized. Each aquarium was covered on all four sides with a styrene sheet and divided lengthwise by a styrene sheet. The styrene is translucent but does not permit a fish a clear view of neighboring fish, allowing the fish to acclimate to the aquaria without inducement of aggressive interactions. Both sides of the aquaria were identical with incoming water and outflow on both sides and each side received equal amounts of food.

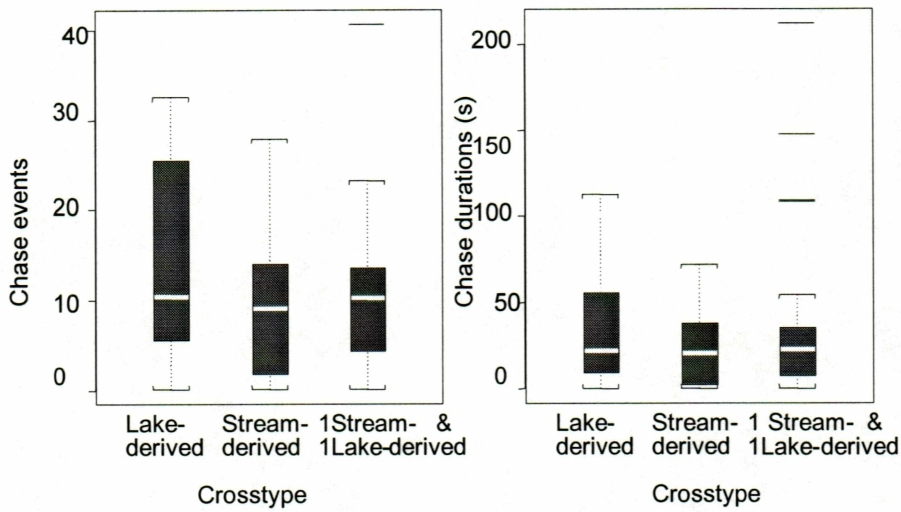

Figure 2: Boxplot of chase data from lake- and stream-derived parr. Chase events and durations(s) performed by two *O.mykiss* parr in aquaria over two ten-minute observation periods. Data points are corrected for observer effects. Aquaria setups were either 2 Lake parr n=35, 2 Stream parr n=37, or 1 Stream & 1 Lake parr n=38. The median of the population is denoted by the white stripe. Whisker span is 1.5 *Inter- Quartile Range. Outliers are shown above whiskers.

To begin the first observation the styrene divider and the styrene aquarium covers were removed. The fish recovered from this intrusion for three minutes before the ten-minute observation began. Observations began upon introduction of food (0.5 grams of #2 crumble Moore Clark™). A second feeding occurred at the halfway point in the observation. The second set of observations did not begin with the removal of the styrene dividers and no three-minute acclimation time was allowed.

The protocol for the fry was the same as for the parr except that the observation length was seven minutes and four unmarked fry were observed in each aquarium. The fry were not acclimated separated by the styrene dividers. The treatments observed were:

four stream-derived fry N=40), four lake-derived fry (N=39), four hybrid lake x stream fry (N=41), four hybrid stream x lake fry (N=40) (Figure 3).

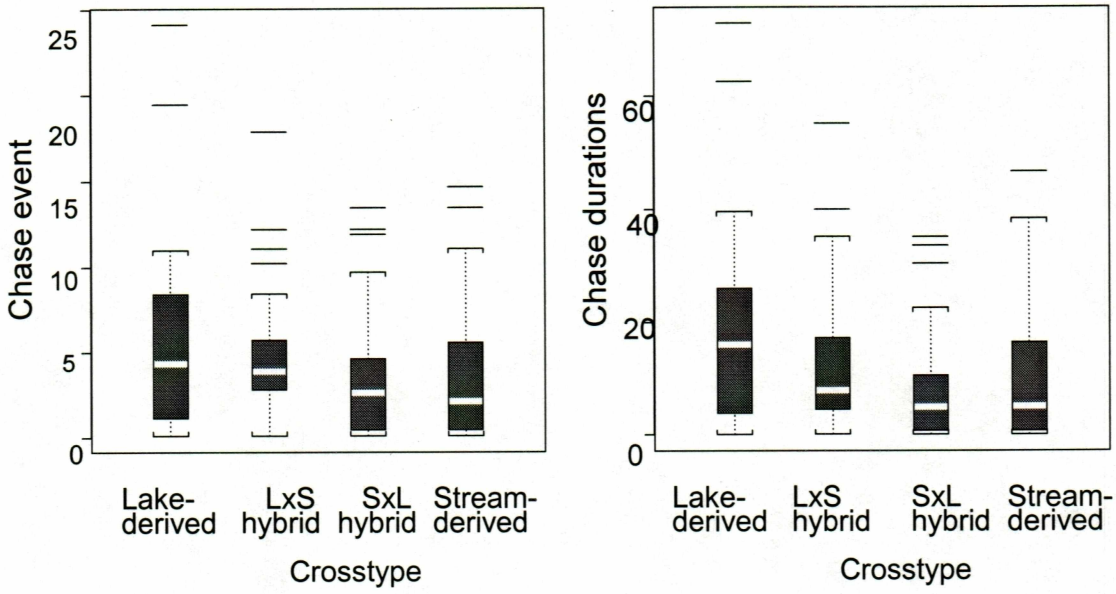

Figure 3: Boxplot of chase data from lake- and stream-derived fry and reciprocal crosses. Chase events and durations(s) performed by four *O.mykiss* fry in aquaria over two seven minute observation periods corrected for observer effects. Aquaria setups were either : 4 Lake fry n= 39, 4 lake x stream hybrids n=41, 4 Stream fry n=40, or 4 stream x lake hybrids n=40. The median of the population is denoted by the white stripe. Whisker span is 1.5*Inter-Quartile Range. Outliers are shown above whiskers.

A two-way analysis of variance was performed on the events as well as the durations data. Factors included in the model were observers χ^1 and crosstype χ^2. The initial model included interactions between the two factors. The experimental design attempted to exclude interaction of crosstype and observer by keeping the observers naïve to the crosstype they were observing, but the factor was tested to see if an uncontrolled

interaction occurred ($\mu=\beta_0+\beta_1\chi_1+\beta_2\chi_2+\beta_1\chi_1\beta_2\chi_2+E_0$). No evidence of significant interaction was seen so a model without interaction was used:
$\mu = \beta_0 + \beta_1\chi_1 + \beta_2\chi_2 + E_0$ (Appendix A&B). For actions in which significant differences between populations were seen ($p \leq .05$) the data were corrected for observer effect (Appendix C) and a Holm multiple comparison test (programmed for S-plus by R. Fagen 2001, Glantz and Slinker 2001) was performed to determine difference between crosstypes. The Holm test used an experiment-wise alpha of 0.05, and p values ≤ 0.01 were considered significant (Appendix D). All analysis was performed with S-Plus (Version 6, Insightful corporation, Seattle, WA).

For the parr trials a test of clip effect was also performed. A t-test was used to compare actions of individual fish in aquaria. In aquaria containing two lake-derived parr (N=35) or two stream-derived parr (N=37) a paired t-test compared the clipped to unclipped for each of the crosstypes. For aquaria that had 1 lake- and 1 stream-derived parr (N=38) a t-test was performed for each crosstype (Appendix E).

A subset of the fry aggression data including only the stream- and lake-derived crosstypes was analyzed separately by ANOVA with observer and crosstype as factors. This allowed comparisons of observations of fry with observations of parr (Appendix F).

Results

Significant differences between the crosstypes occurred only for chasing behavior. Lake-derived parr and fry chased more than stream-derived parr (p=0.005event; Figure 2) and fry (p=0.03 event, p=0.03 duration; Figure 4). In fry trials in which hybrid aggression was also tested, the lake-derived fry (p=0.006 event, p=0.001 duration) and the lake x stream hybrid fry (p=0.009 event, p=0.023 duration) chased more than the stream x lake hybrids (Figure 3).

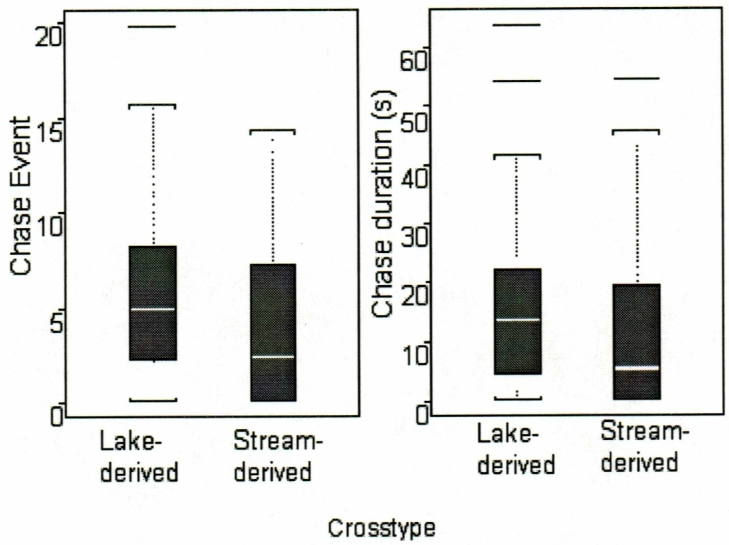

Figure 4: Boxplot of chase data for lake- and stream-derived fry. Chase events and durations (s) corrected for observer effects performed by four *O.mykiss* fry in aquaria over two seven-minute observation periods. Aquaria setups were either: 4 lake-derived fry (n=39) or four stream-derived fry (n=40). This data is a subset of the fry aggression trials. The median of the population is denoted by the white stripe. Whisker span is 1.5 *Inter-Quartile Range. Outliers are shown above whiskers.

Significant differences were detected between observers $p<0.05$ for almost all actions. No interaction was detected between the crosstypes and the observers. The observer effect was most significant for more subtle behaviors (i.e. approaches) and not significant more overt aggressive behaviors (i.e. nips) (Appendix A & B).

The mean number and durations of chase events in aquaria containing one stream-derived and one lake-derived parr fell intermediate between and not different ($p>0.05$) from means in aquaria with exclusively stream-derived or lake-derived parr (Figure 2).

An effect of mark (adipose fin clip) on number of chases was detected in the lake-derived parr by one of the two observers. Lake-derived parr that were clipped chased more when in an aquarium with an unclipped lake-derived parr ($p=0.023$). No significant

mark effect was seen: 1) with the other observer (p=0.07) or 2) when the marked lake-derived parr was in an aquarium with an unmarked stream-derived parr (p=0.35), or 3) when a marked stream fish was paired with an unmarked stream fish (p=0.83) with either observer (Appendix E). This mark effect could discount the finding that lake-derived parr chase more. However, evidence of the same trend in emergent fry (where none of the fish were marked) supports the observation that increased chasing occurs in lake-derived parr regardless of mark effects.

In the fry trials that included hybrid data a two-way ANOVA of chase events and of durations detected differences between crosstypes (p=0.007, p=0.005). The Holm test indicated that lake and lake x stream fry chased more often than the stream x lake fry (Figure 3). A two-way ANOVA of chases by stream-derived and lake-derived emergent fry indicated that the lake-derived fry chased more than the stream-derived fry (p=0. 03 duration and event)(Figure 4;Appendix F)

Fin Condition Trials:

O. mykiss from the 2001 spawning year were raised in 40 micro-vertical raceways (described in Heintz & Joyce 1992), stocked at densities of 500 fry per raceway. The raceways were filled with Sashin Creek filtered water. Each micro raceway had an incoming counter clockwise flow (8L/min). Each crosstype was represented by ten family lines all of which were held in separate micro raceways. Fin condition (fin height/forked length) was calculated for the dorsal fin as well as for the total pectoral fin length (right pectoral length + left pectoral length).

The treatment groups that were examined in this experiment are:

1: stream-derived parr

2: lake-derived parr

3: stream x lake hybrid parr

4: lake x stream hybrid parr

A sample size of 100 fish was taken for each crosstype (ten parr from each family). Total length and all fin lengths were measured with calipers. Measurements were

uniform for all populations, starting perpendicular from the base of the fin (pectoral or dorsal) measuring along the ray of the longest available fin ray.

A sample of ten fish was taken from all ten family lines created for each of the four cross types created. The family lines as well as the cross types were examined. The dorsal fin condition was assessed using the equation: fin condition = dorsal fin length/total length (adapted from Kindschi et al.1987).

Ten family lines were available for each of the four crosstypes (stream-derived, lake-derived, lake x stream hybrid, and stream x lake hybrid). From each of these families a sample of ten parr were collected and preserved in a formalin solution. This resulted in a sample of 100 fish from each crosstype. Fish were collected from the vertical raceways by removing the habitat structure and netting out a small sample of fish from the raceway. Care was taken not to select for bottom-oriented or surface-oriented fish, and to be consistent in sampling.

The fin condition data for each crosstype were compared using a nested ANOVA that examined each of the ten family lines within each crosstype. The nested factor was the family while the main factor was the crosstype of the fish. A Tukey multi-comparison test was used to determine what differences existed between crosstypes (experiment wise alpha=0.05) (Appendix G).

Results

The dorsal fin condition results showed that the stream x lake hybrids and lake-derived parr had statistically significant better dorsal fin condition than the lake x stream hybrids. None of the crosstypes were significantly different from the stream-derived population (Figure 5). Both family and crosstype were seen to be significant ($p<0.0$, Appendix G) in the nested ANOVA performed on the dorsal fin condition data. A Tukey multiple comparison test on the effects of crosstype on dorsal fin condition data (experiment wise alpha=. 05, Appendix G (Figure 5).

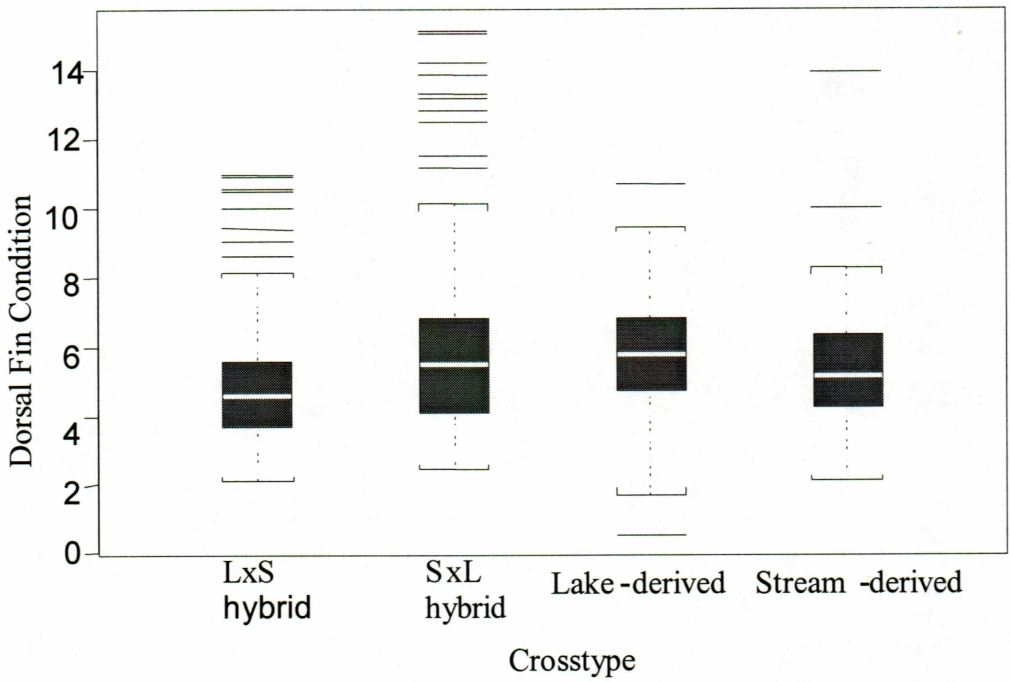

Figure 5: Boxplot of dorsal fin condition. Sample sized for each crosstype were n=100, with each of the ten families for each crosstype contributing 10 individual parr. The median of the population is denoted by the white stripe. The span of the whiskers is 1.5 *Inter- Quartile Range. Outliers are shown above and below the whiskers.

The pectoral fin condition results showed that all crosstypes were significantly different from each other ($p<0.01$) with the order from best to worst fin condition being: lake x stream hybrid, stream-derived, stream x lake hybrid, and lake-derived (Figure 6). Family influences were also highly significant ($p<0.01$, Appendix G).

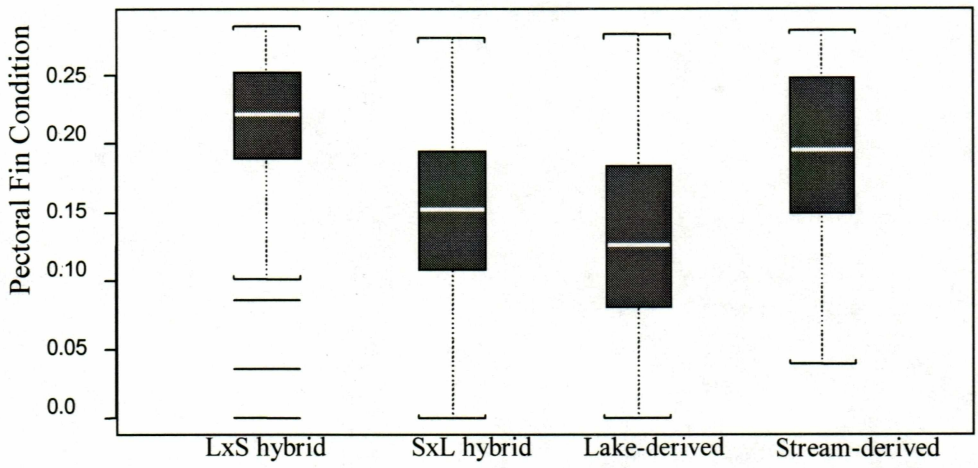

Figure 6: Box plot of pectoral fin condition. Sample sizes for each crosstype were n=100, with each of the ten families for each crosstype contributing 10 individual parr. The median of the population is denoted by the white stripe. The span of the whiskers is 1.5 *Inter- Quartile Range. Outliers are shown above and below the whiskers.

The results from the fin condition experiments, though highly statistically significant (Appendix G), fail to portray meaningful biological significance. The differences seen in the pectoral vs. dorsal fin condition could represent behavioral differences in nip placement between crosstypes or behavioral differences between the crosstypes where different fins are subject to rubbing and degradation. In direct observations of the experimental groups in aquaria pectoral nipping occurred more often than dorsal fin nipping and at times intense nipping aggression did result in substantial pieces of fin being removed from the attacked fish. These events were rare and the normal nip usually resulted in small tears in the fin. It could be that these small tears lead to a degraded fin. The measuring of fin condition should be used as a general assessment of aggression but it only identifies one type of aggression nipping and therefore does not tell a complete story.

The main reason for the lack of biological significance is the small measurable difference seen between the fin conditions. It is unclear how precise the measurement of fin condition is for determination of aggression rates. Because there were relatively few fish that had perfect fin condition in any of the crosstypes comparisons differences in fin height could reflect morphological differences in the population instead of differences as a result of nipping.

The structure of the raceways used in this experiment leave little room for fin degradation by rubbing and the use of shelter in the raceways has improved the fin condition of the fish compared to previous years when no structure was used (F. Thrower, NMFS, 11305 Glacier Highway Juneau, Alaska 99801, USA, personal communication.). However, effects of the rearing environment were seen in the pectoral fin condition where in all crosstypes the right pectoral fin was degraded more than the left. The main hypothesis for this occurrence is that the counterclockwise water flow experienced by all the fish in rearing allowed for fin nipping to occur with greater frequency on the right side. Stocking densities for the family specific raceways were similar, but due to mortalities the densities in the raceways became different over time. However, when fin condition was plotted against the density at time of sampling no relationship was detected.

In order for the fin condition assessments to be more conclusive morphological data should have been collected at various life stages of the *O. mykiss*. The fin condition could be monitored from the time it was perfect and monitored as it becomes degraded. In this way all fin conditions could be compared not to each other but rather to what they used to be. This would be extremely useful especially since morphological differences are common in fish adapting to different environments. For instance, Swain and Holtby (1989) found that lake-type juvenile coho exhibited less color on their dorsal and anal fins, had shallower body shapes, and had pectoral fins placed farther dorsal than stream-type coho raised under similar conditions. Taylor and McPhail (1985) also saw morphological differences in costal and interior strains of coho. Presumably these differences were adaptations that were beneficial to life in stream or lake environments.

Dominance Behavior Trials:

Differences of acquisition of dominance among all crosstypes was observed in aquaria setups containing four parr, including one parr from each crosstype (stream-derived, lake-derived, stream x lake, lake x stream). Differences in acquisition of dominance between stream- and lake-derived parr were also tested in aquaria containing two parr, including one lake- and one stream-derived

For the four-parr trials it was necessary to mark the fish in order to distinguish crosstypes in aquaria. A color tag was chosen. The tags used were Visible Implant Fluorescent Elastomer tags by Northwest Marine Technology ™. The tags were hand injected using hypodermic needles that administered a small line of liquid plastic that hardened after a few hours. On July 30 and July 31, 2002 the fish were tagged above the maxilla for ease of observation and tagging. Four different color tags were used red, orange, blue and yellow. Tag color, size and crosstype were all randomized. The fish not used for the immediate trial were returned to their vertical raceways according to color, size, and cross type. These fish would be used for the next two trials.

From the literature (Berejikian et al. 2000) and preliminary observations it was determined that an assessment of at least 3 minutes would be made in which, if enough evidence was given, a fish would be identified as dominant. The recorded trial would then commence with the actions of the dominant individual being observed. At least 1.5 hours later a final assessment would be made to ensure that the dominant individual observed previously was still the dominant individual. Dominance for each trial was checked a total of three times if dominance was consistent throughout the observations. If the dominant individual changed in any of the observations the observations began anew with the initial 3-minute observation. This method seemed to best identify the dominant fish in each aquarium and protected the observer against mistakes in dominance detection (Table 3).

Table 3. Definitions of dominance during preliminary assessments, observations of dominance and confirmation of observations. Literature references for the definitions.

Definition	References
Preliminary assessment of dominance	
1. Moves freely about the aquarium (i.e., is not inhibited from going into areas because it is another fish's territory)	Berejikian et al. 2000
2. Initiates aggressive actions on other fish without retaliation or being chased	Berejikian et al. 2000
3.prominent parr marks on light shade lateral line	Keenlyside and Yamamoto 1962, Berejikian et al. 1996
Observation of dominant fish	
1. Delivered more attacks than it received	Keenlyside and Yamamoto 1962, Berejikian et al. 2000
2. Never exhibited submissive behavior	Keenlyside and Yamamoto 1962, Berejikian et al. 2000
3.Was never chased out of territory	Keenlyside and Yamamoto 1962, Berejikian et al. 2000
4. Held a prominent feeding station when food or slurry was present, feeds often	Berejikian et al. 2000
Confirmation observation 1-2 hours later	
1. Holds prominent feeding station in the front of feeding tube	Berejikian et al. 2000
2. If aggression occurs is the victor	Keenlyside and Yamamoto 1962, Berejikian et al. 2000

After the first day of observations, the dominant fish was removed from all the aquaria. The dominant fish's tag color was recorded and assigned an appropriate rank. The ranking system gave the first fish removed (the most dominant) a rank of 4. Remaining fish were then allowed to acclimate to their new situation for 15 hours before the aquarium was observed in the same manner the next day with only three fish. The next day with three fish in the aquarium the dominant fishes received a rank of 3. On the final trial day the two remaining fish were observed for dominance and the dominant fish received a rank of 2, and the remaining fish received a rank of 1.

For the two-parr trials (pitting stream- and lake-derived parr) aquaria containing one lake and one stream parr were assessed for dominance according to the "protocol for assessment of dominance" requirements listed under observation of dominant fish in Table 3. The parr in this experiment were identified to crosstype in the aquaria by adipose fin clip which was randomized so that each crosstype experienced the clip.

This experiment was performed on the aquaria that contained 1 lake and 1 stream parr in the aggression experiment after the aggression trials and assessment of dominance was made. Dominance was assessed after the two parr had been exposed to each other for only 15 minutes and the final assessment the fish had been exposed to each other for at least two hours.

A chi square test of independence was used to determine if the presence of a clip on the affected dominance for the two crosstypes. A second chi square test was performed to determine the effect of crosstype on dominance. Both tests were performed for the early assessment and the late assessment.

In the four-parr trials the ranked data was averaged for each crosstype and color collected for each of the three trials (N=19, 18, 6). For example, the stream crosstype would have an average rank for yellow, blue, orange and red for trial 1, 2 and 3. An ANOVA was performed for each trial with crosstype and tagging effect as factors and testing interaction. A final ANOVA was performed for all trials combined with the same factors and testing interaction. For the final ANOVA trials were weighted with the

number of experiments performed in each of the trial (i.e. 19, 18, 6). A Tukey multiple comparison test was performed to determine differences between crosstypes (Appendix H).

Results

In aquaria trials where one stream-derived parr and one lake-derived parr competed for dominance, lake-derived parr were seen to be dominant significantly more often than stream-derived parr with lake-derived parr dominating in 24 out of 35 trials in the final assessment of dominance ($p=0.03$, Figure 7). When stream-derived, lake-derived and reciprocal hybrid parr all competed for dominance in aquaria no difference in dominance acquisition was detected between the stream- and lake-derived parr. However, the lake-derived, stream-derived and lake x stream hybrid all acquired significantly higher ranks of dominance ($p<0.05$) than the stream x lake hybrid according to a Tukey multicomparison test (Figure 8, Appendix E).

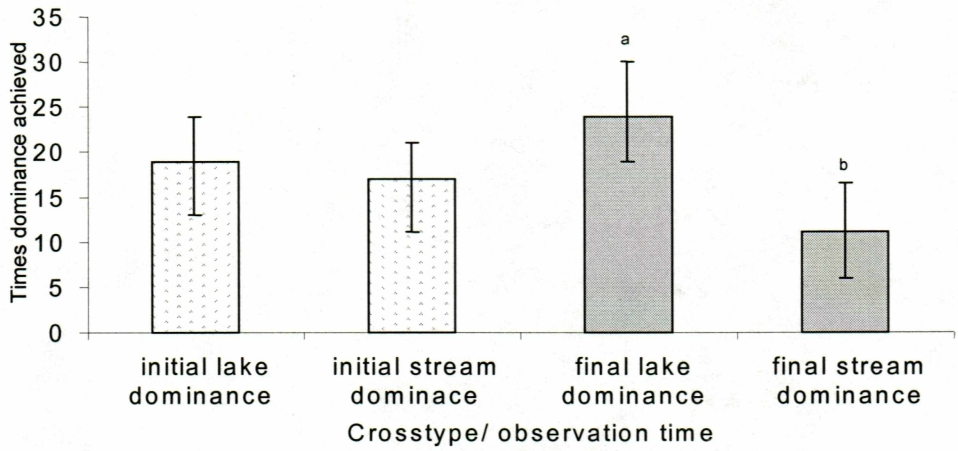

Figure 7: Dominance trials between lake and stream parr. Shown are the number of times either Stream- or Lake derived parr achieved dominance when together in aquaria. The initial assessment was performed 15 minutes after introduction and no significant difference ($p<0.05$) was seen between the two crosstypes. The final assessment was performed 5-6 hours later and a significant difference was seen indicated by the lettering in the figure.

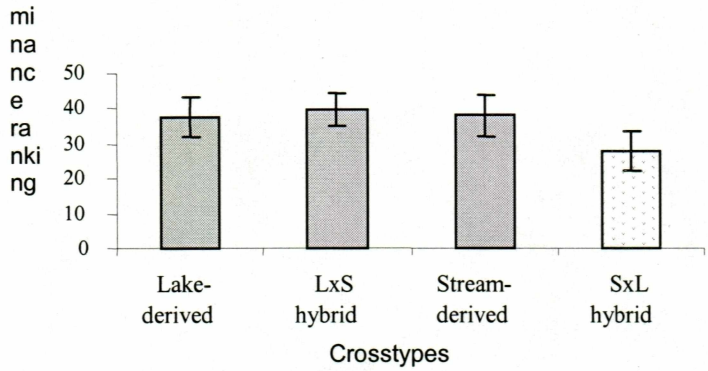

Figure 8:Dominance trials between all four crosstypes. In these trials all four crosstypes competed (n=46). The average ranks earned by each crosstype are displayed above. These ranks were analyzed by two-way ANOVA with mark and crosstype as factors (p=0.006 crosstype). Significant differences ($p<0.05$) were determined by a Tukey multiple comparisons test and indicated by coloring in figure.

The ANOVA tested for the effect marking on the parr (color tag), the effect of crosstype, and interaction between the two factors (Appendix H). No detectable effect of marking was observed (p= 0.179) nor was any significant interaction between marking and crosstype (p=0.169) detected for the compiled data. However, when the three dominance trials were analyzed separately an effect of color was seen in two out of three trials. In trial one the color effect was significant in the ANOVA (n=19, p=0.009). A Tukey multiple comparison test indicated an orange tag assisted in dominance acquisition over a blue, yellow, or red tag ($p<0.05$). In trial number two, color of the tag was significant in the ANOVA (N=18, p=0.002) and a Tukey multiple comparison test indicated that the red tag assisted in dominance acquisition over all other tag colors. In the third and final trial no color effect was detected (N=8, p=0.65). Interaction between color and strain was never significant ($p<0.05$). Color was randomized between strains and no interaction occurred between color and strain. Color tags on the fins have been used for dominance experiments without significant results (p=0.09) (Berejikian et al. 2000). However, the placement of the tag in the maxilla region of the fish could be the

reason that in some of the trials significant effects were seen. It could be that the maxilla is prominently displayed between the dueling fish. Coloration on the head of fish can be a signal in aggressive contests and could be the reason for natural displays of color (e.g. cutthroat trout).

In the dominance trial was performed exclusively on stream-derived and lake-derived parr a chi square test showed that upon introduction there is no significant difference in the acquisition of dominance ($p=0.74$), but with time lake-derived parr acquired dominance more frequently than the stream-derived parr ($p=0.03$, Figure 7). The early assessment of dominance was performed approximately 15 minutes after the fish were exposed to each other and the final assessment occurred 5-6 hours later. Adipose fin clips were used to differentiate the individuals in the aquaria and a chi square test was used to determine if the clip had an effect on acquisition of dominance. No effect of marking was seen in the early assessment ($p=0.77$) or in the final assessment ($p=0.45$).

Predation Trials:

Fifteen micro-vertical raceways (Heintz & Joyce 1992) were filled with Sashin Creek filtered water each with incoming flow at approximately 8L/min. In these raceways the experimental fish acclimated and were exposed to predation via the introduction of Dolly Varden into the raceways.

In these trials the survival of the treatment groups: lake-derived ($N=41$), lake x stream hybrid ($N=37$), and stream x lake hybrid ($N=38$) were compared to the stream-derived fry. All groups were compared to the stream-derived group with the purpose of seeing if deviations from the stream population occur with sequestration in a lake as well as hybridization.

Fifteen trials were performed each day, five with lake-derived, five with stream x lake hybrids, and 5 with lake x stream hybrids. Each micro-raceway contained eight emergent fry: four of the fry were always stream type and the other four were lake-derived or one of the hybrids. An adipose fin clip differentiated the two treatments. The group that received the clip was alternated for each raceway. For example, in raceway 1 the stream fry would all be clipped and in raceway two the "other" type would have the

clip. Location of treatments in raceways was also randomized. After being clipped and size matched (within 2mm fork length) the emergent fry were allowed to acclimate in the vertical raceways for 1 day before the predator was introduced. In previous work it was seen that an overnight acclimation time was adequate to eliminate predator preference for a clipped fish (J. Joyce, NMFS, 11305 Glacier Highway, Juneau, Alaska 99801 personal communication). The emergent fry used for this experiment were all naïve to any predator.

Dolly Varden (*Salvelinus malma*) were used as *O. mykiss* fry predators due to their presence in Sashin Creek and because they will eat *O. mykiss* fry. Dolly Varden predators were caught in Sashin Creek from July 20th to August 1st, average size being 18.8cm (s=1.62). The Dolly Varden were caught with barbless hooks, nets and smolt traps. As the Dolly Varden were caught they were held in vertical raceways and fed a diet of dried fish pellets (Bio Oregon™ 3mm). On August 1st a predator pre-trial was performed to ensure that all the predators would eat *O. mykiss* fry. For the predator pre-trial four *O. mykiss* fry were allowed to acclimate in the vertical raceways on July 31st and on Aug 1st predators were introduced into the raceways. Raceways were periodically checked and the trial was stopped when two of the fry were eaten. If the predators ate two fry they were considered acceptable for use in the experiment. Nine Dolly Varden were excluded from the trials because they did not eat *O. mykiss* fry within the 24 hours of exposure. The remaining Dolly Varden were divided into three groups, group one and two contained 15 Dolly Varden and would be used in the trials and group three contained extra Dolly Varden if replacements were needed in the duration of the trials. The two main predator groups were rotated, each group being the predator for every other trial. The Dolly Varden were starved for 24 hours before beginning a trial.

After the fry were acclimated in the vertical raceways Dolly Varden were introduced at 6:00 am. Immediately following the introduction all raceways were observed for predation. The trials were run until 3-4 fish were eaten or until 48 hours had elapsed. Raceways were checked approximately at 6:00am, 7:00 am, 8:00 am, 10:00 am, 1:00 pm, 3:00 pm, 5:00 pm, 7:00 pm and 9:00 pm. Adjustments were made in

observation times according to how the trials were running. Towards the end of the experiment the predators were getting better at capturing the fry and so the raceways were checked continuously until the quickest predators had consumed 3 fry.

The survival for each crosstype and the corresponding survival of the stream-derived fry for each vertical raceway were analyzed with a Wilcoxon matched pairs signed-rank test (Appendix I). The total numbers of trials for each crosstype were: lake-derived (N=41) lake x stream (N=38), stream x lake (N=37).

Results

The predation trials resulted in no detectable difference between the lake ($p=0.25$) or lake x stream hybrid ($p=0.884$) and the stream-derived parr in their ability to avoid a Dolly Varden predator. A difference was seen where the stream x lake hybrid successfully evaded Dolly Varden predators more often than the stream-derived population ($p=0.036$, Figure 9). These comparisons were performed by the Wilcoxon signed rank test (Appendix I). In observing stream x lake hybrids it can be seen that this hybrid is less aggressive and takes less risks of exposure than the other crosstypes. This less venturous nature could be the reason for its lack of chasing and dominance acquisition but could also have a beneficial side when predation is a concern.

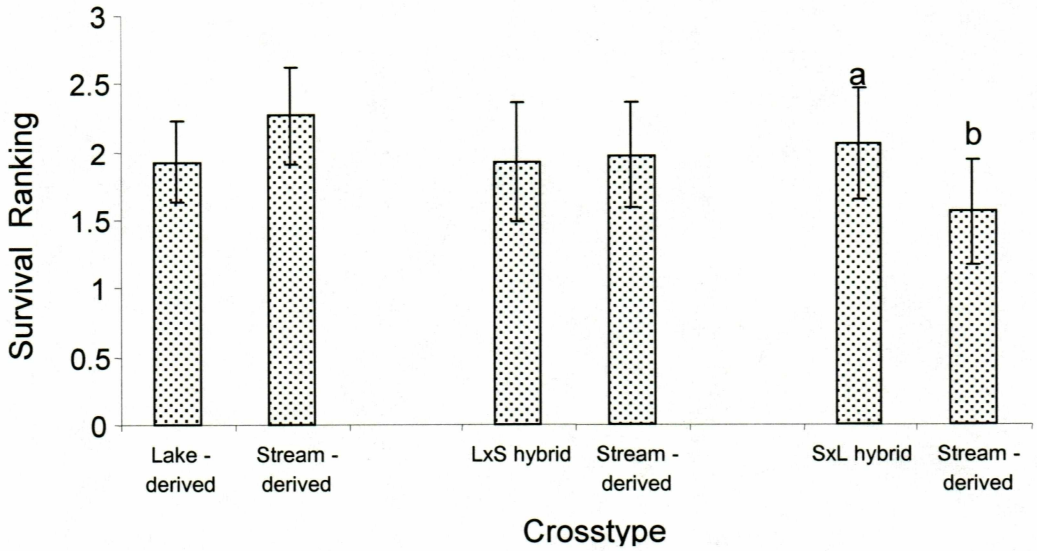

Figure 9: Predation trials performed with a Dolly Varden predator. Shown are the average fry survivals with a Dolly Varden predator of four treatment fry compared to four stream fry controls. A detectable difference was seen between stream and the SxL hybrid p=0.04 using a Wilcoxon signed rank test.

Discussion:

With respect to maintaining fitness-related behaviors of juvenile *O. mykiss*, lake refugia may offer a viable alternative to hatchery conservation. Although differences in chase behavior were detected among the crosstypes, signals used by *O. mykiss* to communicate aggression and dominance were apparently unchanged. All crosstypes exhibited the full spectrum of aggressive actions, it was only the frequency of chases that differed. The chase activity of the lake-derived and lake x stream hybrids was more than the chase activity of the stream-derived and stream x lake hybrids tested, but the magnitude of the difference was not great. The statistical significance of the difference came from consistency of differences between trials rather than the magnitude of differences (Figure 2-4).

Differences of dominance acquisition and predator avoidance could be a concern for managers who are considering the use of lake refuges in conservation if the hybrids are less fit than the parents. Such an inequality could affect the genetic composition of the population because the dominant fish's genes would contribute more to the next generation. In conservation this is an important issue because the native population might be out-competed by the artificially cultured fish and would suffer due to the restoration efforts (Nickelson et al. 1986). In competition among all the crosstypes the stream x lake hybrid had a significantly harder time acquiring dominance than the other crosstypes. This difficulty was also seen in interactions between lake and stream parr in that the lake-derived parr acquired dominance significantly more often than did the stream parr. These findings could have implications for introductions of lake-conserved fish into a stream. However, although there were significant differences in dominance acquisition, all crosstypes established dominance during some trials.

A certain ecological tradeoff was observed in the results from the predation trials, in which the least dominant crosstype, the stream x lake hybrid, was observed to be the best at avoiding predation. This could indicate a greater diversity of life history gained by creation of the stream x lake hybrids. The lack of difference between the lake-derived fry and stream-derived fry indicates that the lake population did not "lose" the genetically based ability to avoid a predator even though they had been without predation for many generations. The artificial environment of the experimental raceways could have contributed to these results as there was little chance for use of cover in the raceways and this strategy, if available, might have been used by the stream-derived crosstype more frequently than by the other crosstypes.

It is clear that there is a genetic divergence between the Sashin Lake population and the Sashin creek populations; however the mechanism causing the divergence is unclear. Three possible mechanisms include i) initial displacement of specific behavioral phenotypes, ii) founder effects or iii) local adaptation to the lake environment. The first could be that the less aggressive transplants into Sashin Lake were displaced from the lake and returned to the stream population. The barrier waterfalls in Sashin Creek blocks

upstream migration of steelhead but allows for downstream migration, thus allowing a one-way gene transfer from the lake to the stream. If the less aggressive *O. mykiss* were displaced downstream this would leave a highly aggressive and dominant population in the lake as well as increasing the number of subdominant and low aggression *O. mykiss* in Sashin Creek. However, the original stocking of the lake is assumed to have been rather small as it was performed by hand, certainly not as many fish as the lake currently supports. The current Sashin Lake population is assumed to be in the thousands and downstream migrations are few (F. Thrower, NMFS, 11305 Glacier Highway, Juneau, Alaska 99801, personal communication). Thus it is unlikely that competition in the lake immediately after stocking would have been severe enough to cause displacement. It is also unlikely that the downstream migrants would have diluted the stream population because only a small number of downstream migrants that would have successfully colonized to the lower creek.

In a conservation application emigration from the lacustrine refuge could be controlled by limiting downstream movement of the transplanted population. Ensuring that the lake provides adequate food and space for the transplanted population could reduce downstream emigration. The carrying capacity of the lake might limit its usefulness as a refuge, but fertilizing the lake might also be an option if the lake's productivity is limited by nutrients. (Crone & Koenings 1985; Oestman 1991).

Another explanation of the divergence of behavior could be that founder population transplanted into Sashin Lake was not representative of the Sashin Creek population in regard to chase activity and social dominance acquisition. While the size of the transplanted population is unknown, a genetic analysis of the lake and stream populations indicated that the founding population for the lake was very small because it was missing some of the rare alleles present in the stream population (Thrower et al. 2003). In a conservation application founder effects could be minimized by transplanting a large representative sample of the source population and minimizing initial mortality immediately after introduction to the lake refuge.

The third possibility is that life in the lake selected for improved survival and reproduction in fish which chased more. Possibly the more mobile feeding patterns adopted in the lake made chasing more common. Without the necessity to guard a single territory in their foraging for food longer and more frequent chases could have become the norm when encountering other fish in the lake. This could cause divergence between the lake and stream populations because abandonment of a territory in the stream environment in order to perform multiple or prolonged chases would involve losing one's station. In this way adaptive divergence in the populations could have occurred, driven by the fitness costs and benefits for each population in its habitat. Chase events, which as defined in this experiment include displacement, could be frequent and advantageous for a foraging lake fish to whom no particular territory is precious. Displacement for a territory holding stream fish could be more costly. In drift-feeding station holding and the ability to defend a territory could directly increase the fitness of a fish. After seventy years of sequestration, the lake fish might have adapted to chasing more in an environment where displacement did not carry much fitness cost. It could also be that in the lake fish commonly use chases as a mid-range aggressive action whereas in a stream, chases are reserved for occasions when a higher level of aggression is necessary. For instance, brook charr from a lake migrating to a tributary stream have been observed to decrease their movement upon entrance to a stream(Biro et al. 1997). Evidence that the divergence is adaptive, not a behavioral response to the fish's immediate habitat, is that hybrids tended to resemble their maternal crosstype in the frequency of chases as well as the duration of time spent chasing (Figure 3). This pattern suggests a maternal effect on the adapted behaviors, not a direct genetic effect that would result in hybrids being intermediate between parents (see stream x lake hybrid Figure 3 and 8).

The increased chasing observed in the lake population could also be attributed to a lack of predation pressure. Many predators of fish are visual predators. Thus sudden movements can catch the attention of predators. This aversion to quick motions may be firmly instilled in the Sashin Creek population by constant predation while the lake population has experienced no such selection. The results of this study do not support this

hypothesis: when faced with actual predation in the predation trials, the lake and stream populations exhibited no difference (Figure 9). However, the containers that these trials were performed in were unnatural in their lack of cover and lack of optimal feeding stations.

Seventy years is not a long period of time for adaptive divergence to have occurred so it would seem that the pressures for divergence in the lake would have had to be quite high to have caused the divergence through genetic adaptation. Local adaptation has been seen to occur very quickly in other transplanted populations (Quinn et al. 2000, Thorpe 1994, Unwin et al. 2003) so it is reasonable to think that selective pressures have been high. In a conservation application of transplantation, knowing that adaptation can occur quickly in transplanted populations, it would be necessary to know what effect these adaptations would have upon re-introduction.

In this experiment it was assumed that the changing population was the sequestered lake population. This assumption was made due to the lack of nearby steelhead populations, however straying from distant populations is a possibility and low rates of immigration can have large effects on a small population. For the Sashin Creek population the chances of straying occurring to the degree that differences occurred between the lake and stream population is quite low.

From the results of this study, which indicate that local adaptation to a lake environment is possible after only seventy years, concerns about the use of this strategy are warranted. If lakes do produce more aggressive and more dominate fish then using them to aid in the recovery of their founding stream population could lead to interaction problems between the two populations and the hybrids they possibly would create. The efforts made for conservation could damage the recovery of the anadromous stream population through increased competition. Furthermore, the lower marine survival (2.66% stream and 0.105% lake) and smoltification rates (68% stream and 50% lakes) of the lake population could result in the re-introduced lake population out competing the stream population in the freshwater only to perish in the marine environment or become residuals. This would create a lower fitness of the stock meant to aid in recovery as well

as being the cause of lower fitness in the stream population. This type of effect has been identified in some of the hatchery stocks used for re-building natural populations (Chilcote et al. 1986, Chilcote 2003). This worst-case scenario should be considered as a possible outcome and weighed against any other possible alternatives before used for the conservation of a population.

There are different scenarios for the use of refuges and in some cases refuges may be used to hold the entire remaining population if the stream environment can support none of the population. In this case there would be no stream population to compete with or formation of hybrids upon re-introduction. In this case the only worry would be the excessive energy used by the more aggressive transplanted population and possible residualization and high marine mortality

Preserving populations in isolated lake or reservoir habitats could be less expensive and time consuming than artificial propagation. The expense of artificial propagation for endangered species is important because the species of salmon most at risk of extinction—chinook salmon (*O. tshawytscha*), sockeye salmon, and steelhead (National Research Council 1996)—must be reared in freshwater for one or more years before smolting and migration to the Pacific Ocean. This long-term care could be prohibitively costly. Furthermore the area available in lakes may allow for much larger breeding populations than is economically feasible in hatcheries, thereby reducing the loss of genetic variability through drift (Allendorf & Phelps 1980; Thrower et al. 2003),and increasing survival through a decrease in culture-density related mortalities such as result from , stress from aggressive interactions and disease. Lakes/reservoirs also would provide a food source for the fish without the cost incurred in a hatchery, an advantage beyond the beneficial effect of retaining foraging feeding behaviors in lake populations.

Further work is necessary to determine if the use of lakes as reservoirs is a realistic solution to conservation problems but it is important to keep in mind that conservation decisions are often made dependent upon alternatives. The use of lakes and

reservoirs could be a better solution to captive rearing in hatcheries but a less attractive alternative than in-stream restoration.

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